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New specimens of *Cyclocystoides scammaphoris* (Echinodermata) from the Upper Ordovician rocks of the American midcontinent with implications for cyclocystoid functional morphology

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Abstract.—New specimens of *Cyclocystoides scammaphoris* Smith and Paul, 1982, are here reported from the Upper Ordovician Platteville Formation of northern Illinois, Plattin and Decorah groups of east-central Missouri, and Lebanon Limestone of central Tennessee. These fossils reveal skeletal details that provide insight into the anatomy of cyclocystoids. Of particular significance is a network of channels that likely originate near the center of the central disk and extend along the oral side of the radial plates, bifurcating distally two or three times before entering the radial facets on the proximal surface of each marginal ossicle. From here, the network enters a series of facet canals that extend upward through each marginal ossicle, exiting in a linear row of pores. The canals are very similar in size and distribution to the nerve canals in living echinoderms. The axes of the canals, which number up to 500 in some specimens, and those of the radial ducts project proximally away from the oral surface at an elevation angle of about 25°, apparently forming a network that could have converged within the upper part of the body cavity. This origin and function are made clear by the connection between the channel on each radial plate and the radial facet canal pores within each marginal ossicle.

Introduction

Cyclocystoids are a rare and enigmatic class of echinoderms that range in age from Middle Ordovician (Berg-Madsen, 1987) to early Carboniferous (Haude and Thomas, 1994). They possess a low-profile, disk-shaped body surrounded by a prominent ring of stout marginal ossicles bordered on their distal edges by small, imbricate plates. Proximal to the ring of marginal ossicles is a central skeletal framework consisting of numerous small, imbricate, channeled ossicles forming a radial skeleton that branches outward from the center of the disk to the proximal edges of the marginal ossicles. Appressed to the radial plates, on the side opposite the radial channels, are numerous annular plates.

The most comprehensive investigation of cyclocystoids to date is that of Smith and Paul (1982). Their monographic study includes observations on skeletal morphology, anatomy, growth, functional morphology, mode of life, stratigraphical and geographical distribution, phylogeny, evolution, and systematics. These authors also provide a historical summary of early cyclocystoid investigations, including those by Salter and Billings (1858), Hall (1872), Bather (1900), Raymond (1913), Begg (1934, 1939), Sieverts-Doreck (1951), Kesling (1963, 1966), and Nichols (1969, 1972). Subsequent investigations have focused largely on cyclocystoid occurrences and diversity of cyclocystoids (Berg-Madsen, 1987; Haude and Thomas, 1994; Smith and Wilson, 1995; Glass et al., 2003; Reich and Kutscher, 2010; Sprinkle et al., 2015; Reich et al., 2017; Ewin et al., 2019; Müller and Hahn, 2019; and Ausich and Zehler, 2022). Skeletal homologies, functional morphology, and life mode are poorly understood because cyclocystoids are rare as fossils and microscopic details of their skeletons generally are not well preserved.

Well-preserved marginal ossicles of *Cyclocystoides scammaphoris* Smith and Paul (1982) from the Platteville Formation of Illinois were described and illustrated by Kolata (1975) and Smith and Paul (1982). Recently, additional marginal ossicles have been discovered in beds of marl in the Mifflin Member of the Platteville Formation near Dixon, Illinois. Many of the new ossicles are weathered free from the lime mudstone matrix, unabraded, and reveal microscopic details of the radial ducts, facet canals, lateral and circumferential channels, and stereom. Also examined and reported here are recently discovered specimens of *C. scammaphoris* from the Plattin and Decorah Groups of east-central Missouri and Lebanon Limestone of central Tennessee. All specimens offer insights into unresolved questions of functional

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morphology for this cyclocystoid species and for cyclocystoids more broadly.

Materials and methods

Photography.—All specimens were photographed with a Canon D60 digital camera. Small specimens (<2 mm) were photographed using a Canon CA6528MP MP-E 65 mm f/2.8 1–5× macro photo lens and larger specimens using a Canon EF-S 60 mm f/2.8 macro USM lens. Focus stacking of images was obtained with an automated macro rail by StackShot, and images were processed with Helicon software. To reveal small skeletal details, many specimens were stained with a wash of diluted non-waterproof black India ink, dried, and coated with ammonium chloride before being photographed.

Repositories and institutional abbreviations.—Type, figured, and other specimens examined in this study are deposited in the following institutions: The Center for Paleontology, Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign (ISGS-PAL22) or University of Illinois Geology Department (UI-X) for specimens accessioned pre-2018; Burpee Museum of Natural History, Rockford, Illinois (BMNH); Field Museum of Natural History, Chicago, Illinois (PE).

Systematic paleontology

Phylum Echinodermata Klein, 1778
Class Cyclocystoidea Miller and Gurley, 1895
Family Cyclocystoididae Miller, 1882

Remarks.—For the most part, we follow the morphologic terminology proposed by Smith and Paul (1982). Many of their terms are useful as points of reference in the descriptions and interpretations that follow in this report. However, we disagree with their interpretation of living orientation. We apply the terms "oral" to the cupule-bearing surface and "aboral" to the non-cupule-bearing surface to standardize terminology that does not depend on functional or life habit interpretations. For convenience, we refer to the oral surface as "upper" and aboral surface as "lower" as needed when describing relative positions of features within the cyclocystoid skeleton that lie neither on the oral surface nor on the aboral surface.

Genus *Cyclocystoides* Salter and Billings, 1858

Type species.—*Cyclocystoides halli* Billings in Salter and Billings, 1858 p. 86, pl. X, figs. 2–4, figs. 1, 6, 7 (lectotype GSC 1416a designated by Raymond, 1913) from the Upper Ordovician Cobourg Beds, Ottawa, Canada, by original designation.

Cyclocystoides scammaphoris Smith and Paul, 1982
Figures 1–7

1975 *Cyclocystoides* sp. aff. *C. halli* Billings; Kolata, p. 57, pl. 11, figs. 1–8, pl. 13, figs. 1–4; text-figs. 16, 17.

1982 *C. scammaphoris* Smith and Paul; fig. 16 (1), pl. 17 c, e–g, pl. 19, 68–72, 74.

Holotype.—Partial ring of marginal ossicles with lower disk and peripheral skirt (UI X-4956) from the Grand Detour Member, Platteville Formation, northern Illinois, United States (Kolata, 1975, pl. 11, figs. 2, 4, 8; Smith and Paul, 1982, figs. 16 (1), 17c, e–g, 19, 68–72, 74).

Occurrence.—Mifflin and Grand Detour Members of the Platteville Formation, Turinian Stage, Upper Ordovician Series in north-central Illinois; Zell Member, Macy Limestone Formation, Plattin Group, Turinian Stage, Upper Ordovician Series in eastern Missouri; Spechts Ferry Formation, Decorah Group, Turinian Stage, Upper Ordovician Series in eastern Missouri; and Lebanon Limestone, Stones River Group, Turinian Stage, Upper Ordovician Series in central Tennessee (see Appendix).

Description.—*Cyclocystoides scammaphoris* Smith and Paul, 1982 is here redescribed in detail on the basis of new material. Preserved skeletal structures described here include: (1) composite central disk consisting of radial and interradial plates and annular plates, (2) marginal ring of ossicles, and (3) peripheral skirt (Figs. 1–6).

Central disk (Figs. 1.1–1.4, 2.1, 2.2, 6.5): five or six centrally positioned primary radial plates surrounding depression containing two or three small wedge-shaped plates. Primary radial plates give rise to series of radial plates that bifurcate two or three times distally. Radial plates elongate, imbricate, bifurcate, uniserial with channel on upper surface, and distally connected to marginal ossicles. In holotype (UI X4956), channel is overlain by small, irregularly shaped ossicles (T-shaped plates of Kolata, 1975 and cover plates of Smith and Paul, 1982). Terminal radial plate ("spear-shaped plate" of Kolata, 1975) domed upward with wide channel on lower surface (Fig. 1.2) and possessing short, lateral projections, giving plate star-shaped appearance. Radial plate series flanked by single series of interradial plates that do not bifurcate. Sutural pores round to ovoid in outline and relatively large; positioned between adjacent radial and interradial plates. Annular plates tightly packed, round to oval in outline, central pore aligning with sutural pores (Fig. 6.5).

Marginal ring (Figs. 1–6): 30 to 32 ossicles in largest specimens (Figs. 2.1, 3.1) but fewer ossicles in small specimens (Fig. 3.2). Marginal ossicle height 80% of length. Oral surface covered with numerous prominent pustules that are largest near ossicle crest; wide gap between adjacent marginal ossicle crests. Typically, two cupules per marginal ossicle, but some specimens have one or as many as five. Specimens possessing complete circlet of marginal ossicles commonly have five evenly spaced groups of ossicles with three cupules that appear to reflect inherent pentaradial symmetry (Figs. 2.1, 3.1). Cupules lack tubercles and are deeply excavated (Fig. 6.4); each cupule gives rise to single radial duct approximately 0.1 mm in diameter with axis projecting proximally away from the oral surface at elevation angle of about 25° relative to aboral surface of marginal ossicle (Fig. 4). Some marginal ossicles have

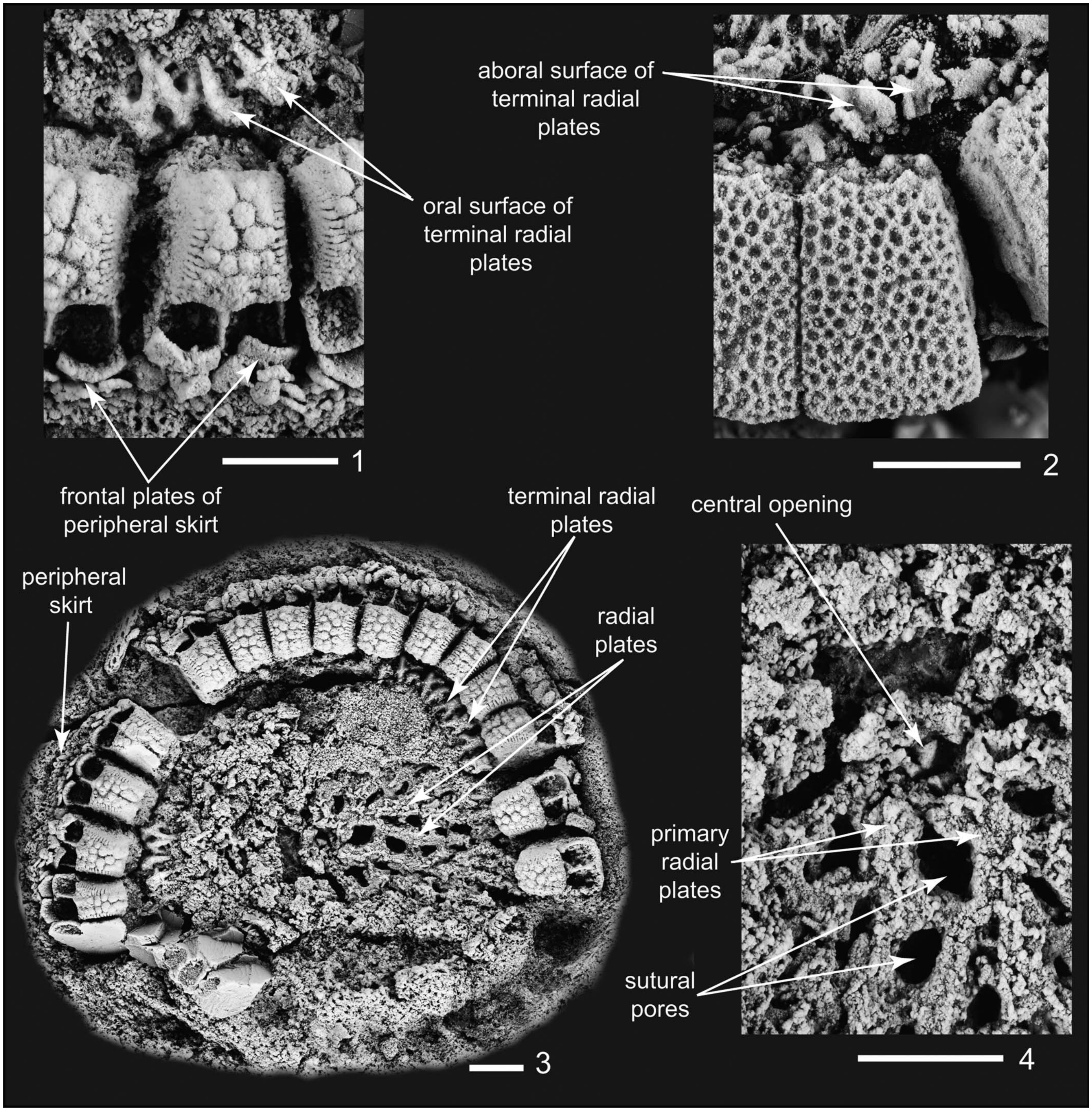

Figure 1. *Cyclocystoides scammaphoris* Smith and Paul, 1982 from Grand Detour Member of Platteville Formation, Dixon, Lee County, Illinois. (**1, 3, 4**) Holotype UI X4956, locality 1: (**1**) oral surface showing terminal cover plates and peripheral skirt with frontal plates; (**3**) full oral view of holotype showing peripheral skirt, terminal cover plates, and radial plates; (**4**) enlargement of holotype showing central opening, primary radial plates, and sutural pores. (**2**) Paratype UI X4957, locality 4, aboral surface showing flat, pitted surface of marginal ossicles and aboral surface of several terminal cover plates showing central groove. Scale bars = 1 mm.

circumferentially oriented linear indentation on proximal side just above radial ducts (Fig. 6.3). Aboral surface relatively flat except for slight upturn along distal and proximal edges; densely covered with small pits; lateral edges in contact with adjacent marginal ossicles. In well-preserved specimens, ossicle surface displays stereom microstructure showing extended trabeculae (Fig. 5.1–5.6). Lateral surfaces have two prominent, centrally positioned regions of linear articulation ridges inclined at ~30°. Perpendicular to articulation ridges is range of lateral striae positioned along oral edge of ossicle. Lateral channels extend distally beginning at lower inside edge of each marginal ossicle and gradually curve upward to join circumferential channel just above cupules. Lateral channels on pairs of adjacent marginal ossicles form tube-like passageway that bifurcates, one smaller branch extending laterally to peripheral skirt and other up to circumferential ring (Figs. 5.1, 6.4).

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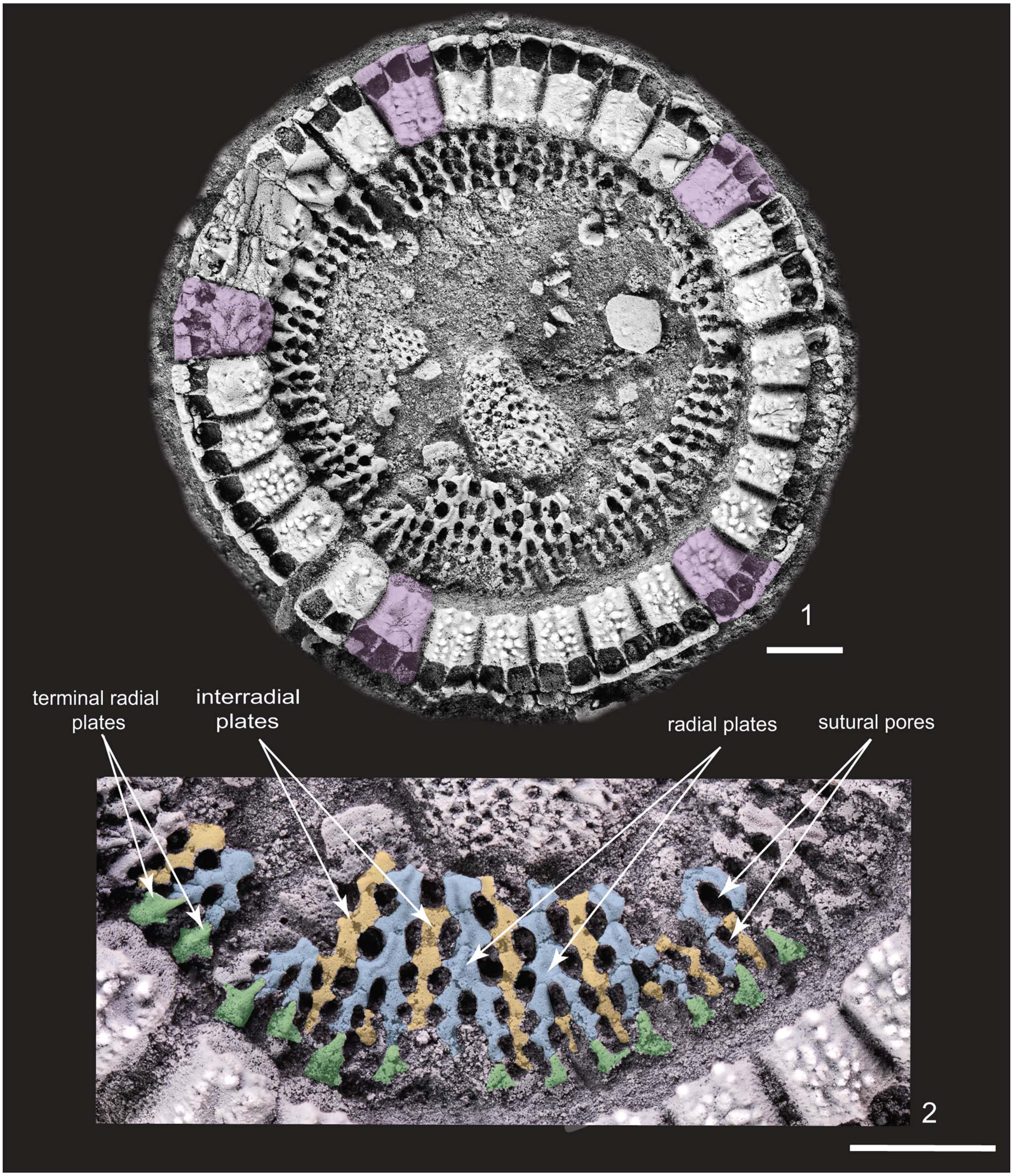

Figure 2. *Cyclocystoides scammaphoris* Smith and Paul, 1982 from Lebanon Limestone, Rutherford County, Tennessee, locality 8. (**1**) Oral view of central disk in specimen PE93328 showing pentaradial arrangement of three-cupule marginal ossicles with three cupules (purple). (**2**) Enlargement of central disk in specimen PE93328 showing radial (blue) and interradial (yellow) plates, terminal cover plates (green), and sutural pores. Scale bar = 1 mm.

Marginal ossicles penetrated by network of internal microscopic canals that terminate at ossicle surface as pores referred to as "upper and lower pits" by Kolata (1975) and "facet canals" by Smith and Paul (1982). Canals approximately 0.06 mm in diameter present in proximal region of marginal ossicles. Facet canals vary in number from 6 or 7 in small marginal ossicles (Fig. 5.4) to 20 or more in larger ossicles (Fig. 6.1). Erosion of proximal face of marginal ossicle in specimen

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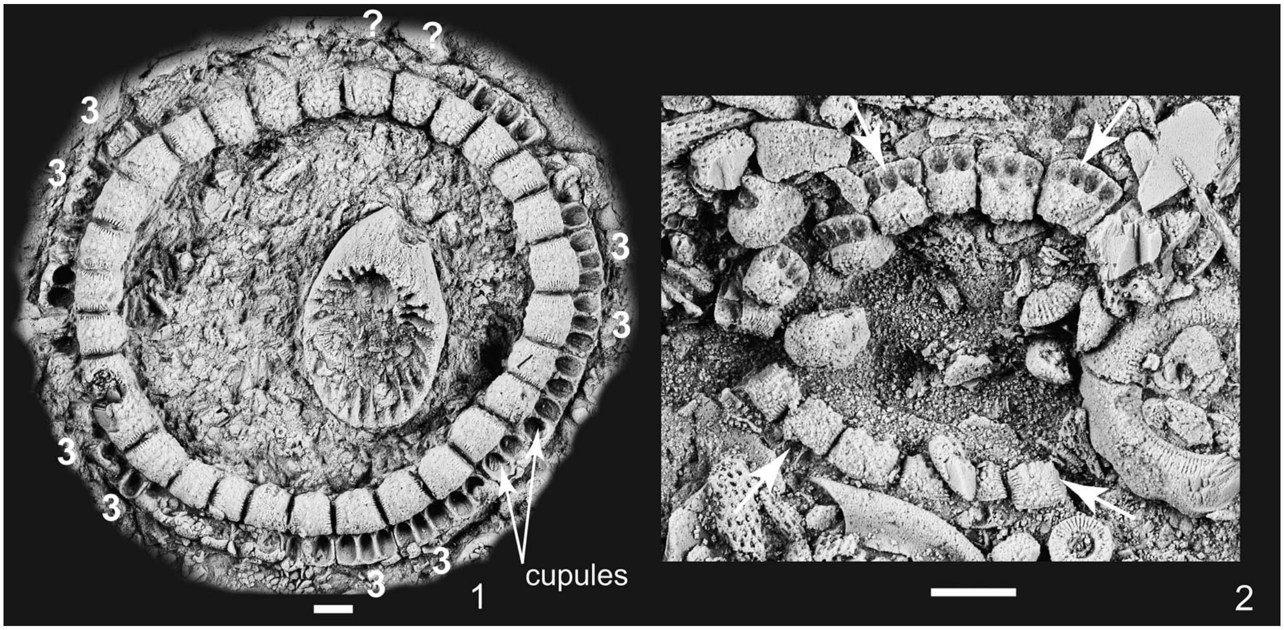

Figure 3. *Cyclocystoides scammaphoris* Smith and Paul, 1982 from Castlewood Limestone Member of Spechts Ferry Formation, Jefferson County, Missouri, locality 6. (**1**) ISGS-PAL22-41 oral surface of complete ring of marginal ossicles showing pentaradial arrangement of paired three-cupule marginal ossicles with three cupules. (**2**) ISGS-PAL22-42 oral surface of incomplete ring of marginal ossicles shown with arrows, each unobscured ossicle exhibiting a cupule count of three or four. Scale bars = 1 mm.

ISGS-PAL22-45 exposes internal network of canals revealing connection between upper and lower series of openings (Fig. 6.2). One specimen (Fig. 4) shows evidence that facet canal is bifurcated and possibly connected to distal regions of marginal ossicle. Facet canals permeate proximal part of marginal ossicle, extending upward internally from a depression inside radial facet to just below radial ducts where they diverge and form a single horizontal row of evenly spaced pores (Fig. 5.3–5.6). Number of pores within radial facets generally equal to number of corresponding pores just below radial duct.

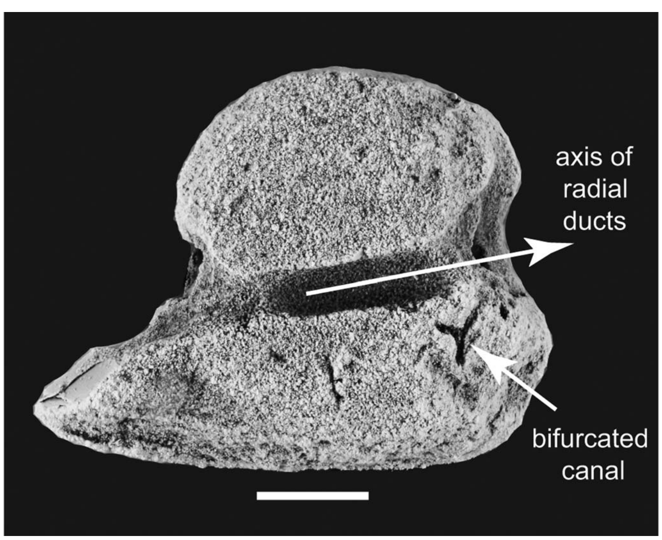

Figure 4. *Cyclocystoides scammaphoris* Smith and Paul, 1982 from base of Castlewood Limestone Member of Spechts Ferry Formation, Jefferson County, Missouri, locality 6: lateral surface of deeply weathered marginal ossicle ISGS-PAL22-43 showing proximal of radial duct and apparent bifurcated radial facet canal. Scale bar = 1 mm.

Axes of canals at upper pore openings project proximally away from the oral surface at elevation angle of about 25° relative to aboral surface of marginal ossicle, parallel to axes of radial ducts (Fig. 5.3). Pore openings visible on upper surface of marginal ossicle (Fig. 5.6). Canal openings within each radial facet arranged in two tightly packed vertical rows beneath adjacent terminal radial plate of central disk (Figs. 5.4, 6.1). Distal edge of terminal radial plate articulates with inverted-U-shaped radial facet on proximal edge of associated marginal ossicle (Fig. 5.3); terminal radial plate bears groove on lower surface (Fig. 1.2) that forms hood over tissue entering facet canals. Proximal edge of terminal radial plate onlaps distal edge of proximally adjacent radial plate (Fig. 5.3, 5.6). It appears that distalmost radial plates extend beneath the terminal cover plates into curved facets along proximal edges of aboral surfaces of the marginal ossicles (Fig. 5.3). Imbrication of radial and interradial plates continues toward center of disk.

Peripheral skirt (Fig. 1.3): Periphery of marginal ring ossicles enclosed by numerous small, imbricate ossicles that decrease in size distally. Proximal or frontal plate is largest in skirt, curved, stands erect or folded down; articulated with distal edge of cupule. In lost paratype BMNH DK-69 (Kolata, 1975, pl. 11, fig. 1), part of the skirt is turned up, covering the cupules.

Remarks.—In the preceding species description, we provide skeletal details for *C. scammaphoris* but have nothing to add or change in the original species diagnosis given by Smith and Paul (1982).

Discussion

Facet canals and nervous system.—This network of canals in cyclocystoid marginal ossicles was described and illustrated

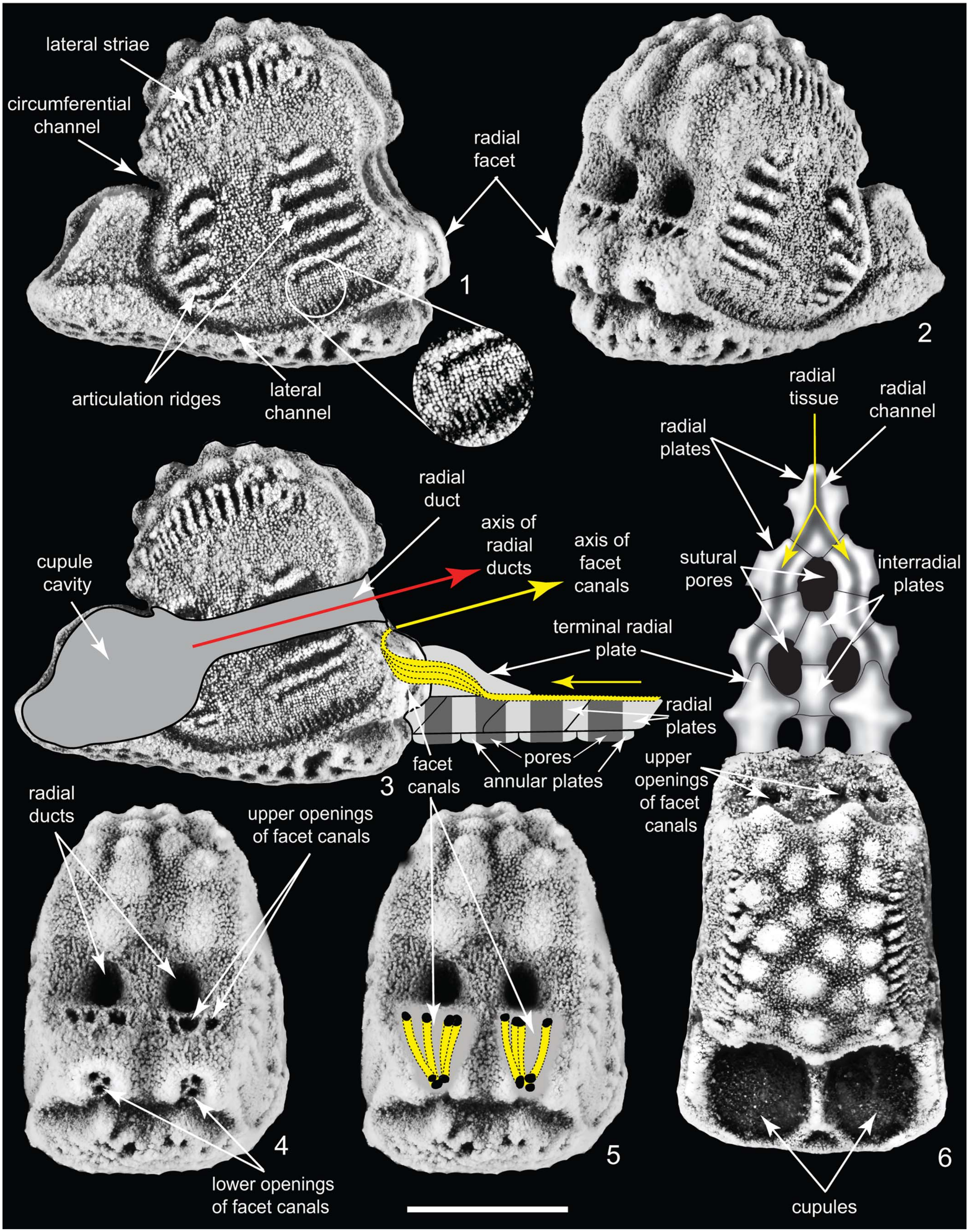

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Figure 5. *Cyclocystoides scammaphoris* Smith and Paul, 1982 from Mifflin Member of Platteville Formation, Dixon, Lee County, Illinois, locality 3. (**1–6**) Topotype ISGS-PAL22-44, a well-preserved marginal ossicle showing microscopic surface details: (**1**) lateral surface showing articulation ridges, lateral striae, circumferential channel, lateral channel, and radial facet, with an inset revealing stereom microstructure with extended trabeculae; (**2**) perspective view showing radial facets; (**3**) lateral view showing cutaway of internal cupule cavity and radial duct (light gray); red arrow shows axis of radial duct; yellow arrows show network of tissue along axis of radial channels entering facet canals positioned below the terminal radial plate and then projecting upward parallel to axis of radial ducts; network of internal facet canals shown in yellow; aboral surface of central disk consists of radial and interradial (not shown) plates underlain by thin annular plates with central pores that aligns with the sutural pores; (**4**) proximal side of marginal ossicle showing radial ducts and upper and lower openings of facet canals; (**5**) cutaway of proximal side of marginal ossicle showing path of internal facet canals in yellow; (**6**) oral surface of marginal ossicle showing cupules and upper openings of facet canals; upper part of figure is an artistic depiction of the terminal cover plates, channeled radial plates, interradial plates, radial channels, and sutural pores; yellow arrows mark the positions of inferred radial tissue that extended along the channels on the oral surfaces of the radial plates from the center of the disk into the facet canals beneath the terminal cover plates. Scale bar = 1 mm.

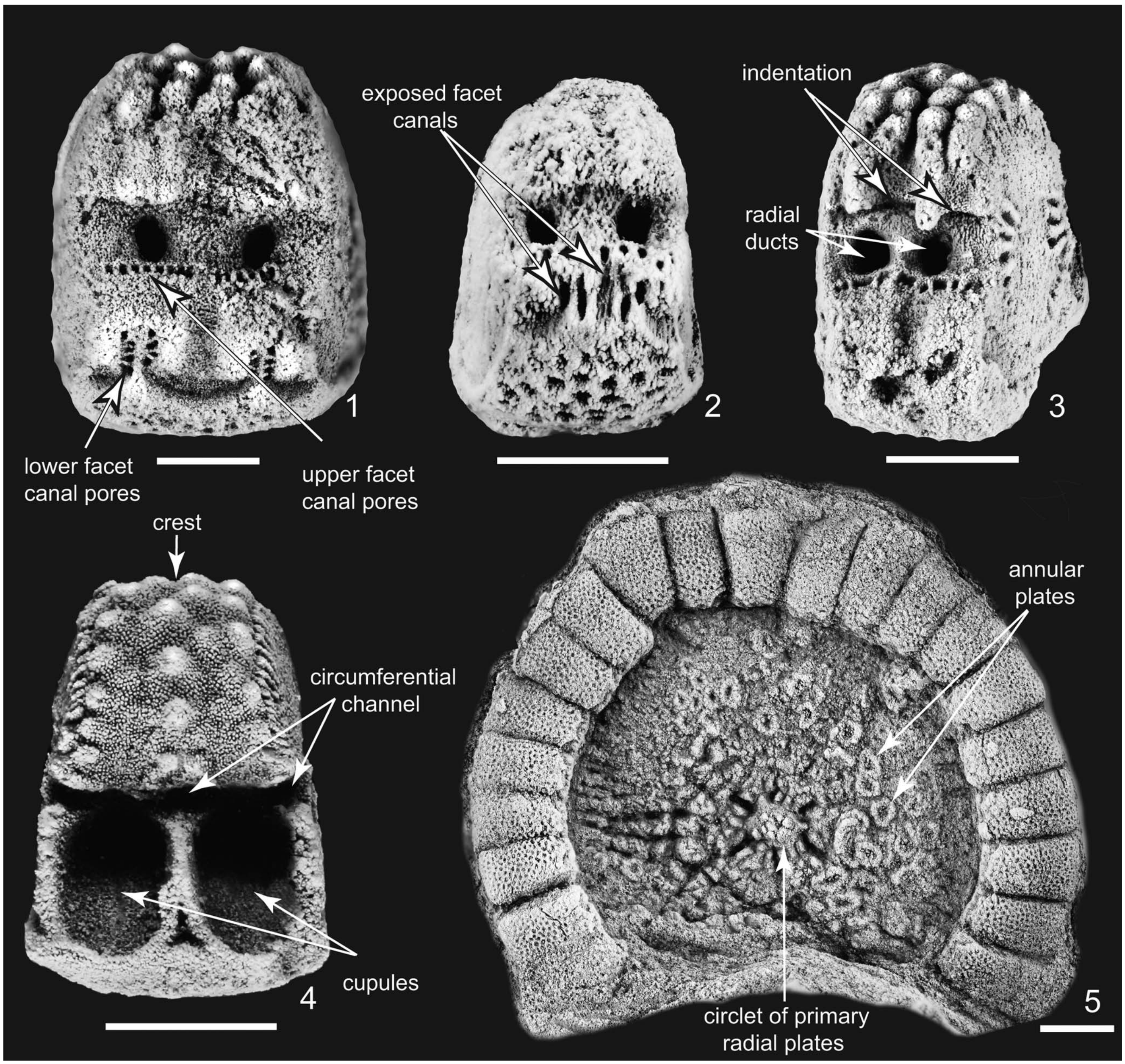

Figure 6. *Cyclocystoides scammaphoris* Smith and Paul, 1982 from Mifflin Member, Platteville Formation, Dixon, Lee County, Illinois. (**1**) Paratype UI X–5097, locality 1, proximal surface of a relatively large marginal ossicle showing numerous upper and lower facet canal pores. (**2**) Topotype ISGS-PAL22-45, locality 2, proximal surface of marginal ossicle showing exposed facet canals connecting upper and lower facet canal pores. (**3**) Topotype ISGS-PAL22-46, locality 2, proximal side of marginal ossicle showing radial ducts and prominent indentation. (**4**) Topotype ISGS-PAL22-44, locality 3, distal surface of marginal ossicle showing cupules and the circumferential channel. (**5**) Paratype ISGS-PAL22-48, locality 4, aboral surface showing marginal ossicles, annular plates, and circlet of primary radial plates. Scale bars = 1 mm.

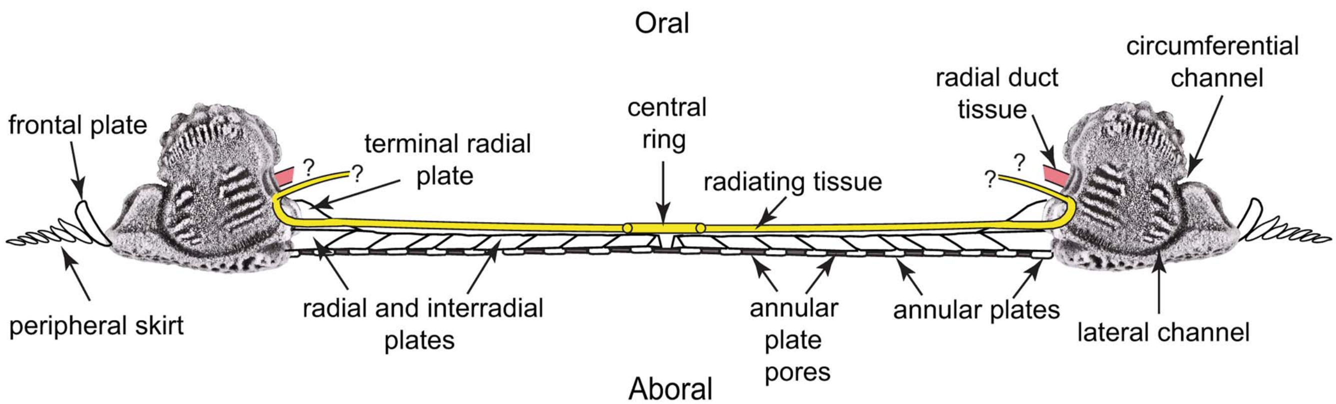

Figure 7. *Cyclocystoides scammaphoris* Smith and Paul, 1982 from Platteville Formation, Dixon, Lee County, Illinois, locality 3: diagrammatic cross section through body center showing reconstruction of marginal ossicles with peripheral skirt, frontal plates, radial ducts, and circumferential and lateral channels as well as oral and aboral orientation. Central disk is composed of radial and interradial plates, annular plates, annular plate pores, and terminal radial plates. Tissue radiating from central ring (yellow) and radial duct tissue (pink) show the implied orientation of tissue projecting up from the facet canals and radial ducts.

by Smith and Paul (1982, p. 602, pl. 11, fig. 180). The canals likely held a network of specialized tissue that originated near the center of the central disk and bifurcated distally two or three times before entering the marginal ossicles. This origin and function are made clear by the connection between the channel on each radial plate and the radial facet canal pores within each marginal ossicle. It should be noted that the terminal radial plate has a groove on its oral surface (Fig. 1.2) that would have formed a hood over the tissue entering the facet canals. The network continued upward through the facet canals, exiting the marginal ossicles just below the prominent radial ducts. The size and distribution of the facet canals are comparable to those of the nerve canals in skeletal ossicles of living crinoids and ophiuroids (Smith and Paul, 1982; Holland et al., 1991) and would not be unexpected in cyclocystoids. Conceivably, a nervous system in cyclocystoids would have originated from a nerve ring positioned near the center of the upper surface of the central disk. Accordingly, the nerves branched out along the channels of the radial plates, passed below the terminal radial plates into the marginal ossicles, and then continued internally upward to just below the interior opening of the radial ducts (Fig. 5.3, 5.5).

The axes of the facet canals and radial ducts project proximally away from the oral surface at an angle of approximately 25° relative to the aboral surface of each marginal ossicle. A single marginal ossicle in *C. scammaphoris* can have as many as 16 facet canals and two radial ducts (Fig. 6.1). For a specimen having 32 marginal ossicles, this would amount to more than 60 radial ducts and 500 facet canals all pointing proximally away from the oral surface. This arrangement suggests that the tissue occupying the radial ducts and facet canals also continued proximally away from the oral surface to form a dome-like network that would have converged within a space positioned above the radial plates (Fig. 7).

Channeled radial plates and water vascular system.—In addition to the nerve tissue, the channeled radial plates likely contained the radial vessels of the water vascular system. Accordingly, the network emanated from a centrally positioned ring canal and followed the radial channels to the proximal side of the marginal ossicles. At this point, some branches of the radial canals and nervous system would be in line with, and possibly would continue into, the lateral channels of adjacent marginal ossicles.

Lateral and circumferential channels on the marginal ossicles.—The lateral and circumferential channels were observed by Kolata (1975, fig. 17) in *Cyclocystoides scammaphoris* and postulated to have contained elements of the water vascular, nervous, or hemal systems. These appear to be the same channels as the "marginal sutural pores" described by Ewin et al. (2019) in *Perforocycloides nathalieae* from the early Silurian of Anticosti Island, Quebec, Canada.

Body cavity.—An upper disk was proposed by Kolata (1975) on the basis of the upward projection of the radial ducts in *C. scammaphoris*. This interpretation was rejected by Smith and Paul (1982) in favor of a body plan consisting of a central disk with two layers, one of radial and interradial plates and the other of thin polygonal annular plates. In their cross section of *C. tholicos* Smith and Paul, 1982 (p. 582, fig. 1b), the annular plates are portrayed as very thin and in contact with the radial and interradial plates. Smith and Paul (1982) stated that the body cavity "was at most only a narrow space separating" the two layers (p. 592) and further that this "precludes extensive internal tissue" (p. 579). Such a reduced body cavity is unlike that in known echinoderms. Alternatively, the proximal projection of radial ducts and facet canals upward away from the radial/interradial plates in *C. scammaphoris* (Figs. 5, 7) suggests that an upper disk may have been present. Accordingly, the body cavity could have been encapsulated by: (1) a non- or weakly calcified upper disk, (2) the marginal ossicles, and (3) a lower disk of radial-interradial plates, including annulars if present. Additional evidence is needed to confirm or negate this hypothesis.

Life mode.—Cyclocystoids commonly occur in association with an abundant and diverse marine fauna in carbonate and siliciclastic rocks that were deposited in subtidal marine environments. Seafloor substrates ranged from firm to unstable, and the environments were generally characterized by significant infaunal and epifaunal activity. The most stable orientation and likely living position of cyclocystoids would have been with the peripheral skirt, flat (aboral) surface of the marginal ossicles, and annular plates of the central disk all resting on the substrate (Fig. 7). In this position, the vaulted crests of the marginal ossicles with prominent pustules and cupules faced upward in the water column.

Conclusions

An extensive network of facet canals within the marginal ossicles is present in specimens of *Cyclocystoides scammaphoris* Smith and Paul, 1982 from the Upper Ordovician rocks of north-central Illinois, east-central Missouri, and central Tennessee. The distribution and orientation of the canals can be observed and mapped in marginal ossicles whose proximal surface is carefully excavated or eroded. The network extends from below the terminal radial plates on the upper surface of the radial plates into the facet canals in the proximal face of each marginal ossicle and then upward through the ossicle interior. The canals exit the ossicle in a linear series of pores situated just below the radial ducts. This network of facet canals is also present in *Morrocodiscus smithi* Reich et al. (2017, fig. 7.8) and *Sievertsia devonica* (Sieverts-Doreck, 1951) as figured by Smith and Paul (1982, plate 7, fig. 117), and we predict its presence in all cyclocystoids. These observations pave the way for future work that further clarifies cyclocystoid functional morphology and life mode.

Acknowledgments

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Declaration of competing interests

The authors declare none.

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Appendix

Cyclocystoides scammaphoris specimens described here are from Upper Ordovician rocks in three regions of the American midcontinent. The first group of specimens includes the type specimens and newly discovered marginal ossicles from the Mifflin and Grand Detour members of the Upper Ordovician Platteville Formation in north-central Illinois (Fig. S1). The second group is a suite of recently discovered specimens from the Upper Ordovician rocks of east-central Missouri (Fig. S2). Notable cyclocystoid-bearing stratigraphic units include: (1) the upper two meters of the Zell Member, Macy Limestone Formation, Plattin Group, (2) the Castlewood Limestone Member (Deicke K-bentonite Bed at base), Spechts Ferry Formation, Decorah Group, and (3) the portion of the Glencoe Shale Member immediately below the Millbrig K-bentonite Bed, Spechts Ferry Formation, Decorah Group. The Missouri cyclocystoids occur primarily as disarticulated marginal ossicles and rarely as complete marginal rings of ossicles. Some bedding planes contain tens to hundreds of marginal ossicles per square meter, varying from well preserved to deeply weathered and lacking surface details. The third occurrence of *C. scammaphoris* is in the Upper Ordovician Lebanon Limestone of the Stones River Group of central Tennessee (Fig. S3). All specimens occur within the *Phragmodus undatus* Conodont Biozone.

In this work, the stratigraphic framework follows Kolata (2021) for Illinois, Thompson (1991) for Missouri, and Wilson (1949) for central Tennessee. The Missouri cyclocystoids occur in association with the Deicke and Millbrig K-bentonite beds, two of the most widespread and well-documented volcanic ash beds in North America (Kolata et al., 1986, 1996). Uranium–lead dating of the Deicke K-bentonite Bed yields an age of 453.35 ± 0.10 Ma (Herrmann et al., 2021). The Millbrig K-bentonite is a confirmed Ordovician Global Boundary Stratotype Section and Point (GSSP) marking the boundary between the Turinian and Chatfieldian stages of North America (Bergström et al., 2009) and has been dated to 452.86 ± 0.29 Ma (Sell et al., 2013). These stratigraphic relations support assignment of the Platteville Formation and Plattin Group to the North American Turinian Stage of the Mohawkian Series and the global Sandbian Stage of the Upper Ordovician Series. The Decorah Group strata of interest in this study lie below the Millbrig K-bentonite and are thus of Turinian age, while Decorah Group strata lying above this K-bentonite are of Chatfieldian age.

Northern Illinois localities

1. Dixon Crusher East Quarry: 4 km north of Dixon, Lee County, Illinois; 41°51′54.31″N, 89°26′29.76″W. Grand Detour Member, Platteville Formation.
2. Dixon Crusher Northwest Quarry: 4 km north of Dixon, Lee County, Illinois; 41°52′50.30″N, 89°27′10.34″W. Mifflin Member, Platteville Formation.
3. Dixon Northwest Quarry: 5 km north of Dixon, Lee County, Illinois; 41°53′32.34″N, 89°27′58.97″W. Mifflin Member, Platteville Formation.
4. Trask Bridge Road: Quarry on north side of State Route 70, 5.8 km southeast of intersection of State Routes 70 and 75 near Durand, Winnebago County, Illinois; 42°22′35.72″N, 89°17′11.05″W. Forreston Beds, Grand Detour Member, Platteville Formation.
5. Stratigraphic column based on a drill core and gamma-ray log from the Illinois State Geological Survey No. 1 Jerry Stuff exploratory boring (API 121412600200) drilled in a small quarry on the west side of Lowell Road, 9 km north of Dixon, Illinois, 41°56′30.76″N, 89°29′39.36″ W. The entire Platteville Formation is present in this drill core.

East-central Missouri localities

6. Route M near Lemay Ferry Road overpass: Outcrop on both sides of Missouri Supplemental Route M about halfway between the Interstate 55 Barnhart exit and the Missouri Route 21 exit; 38°21′43.7′′N, 90°28′16.6′′W.
7. Fox Creek Road: Outcrop previously described by Kolata et al. (1986) and Thompson (1991) on both sides of Fox Creek Road 1 km west of Allenton Road in Eureka, St. Louis County, Missouri; 38°30′16.3′′N, 90° 41′24.8′′W.

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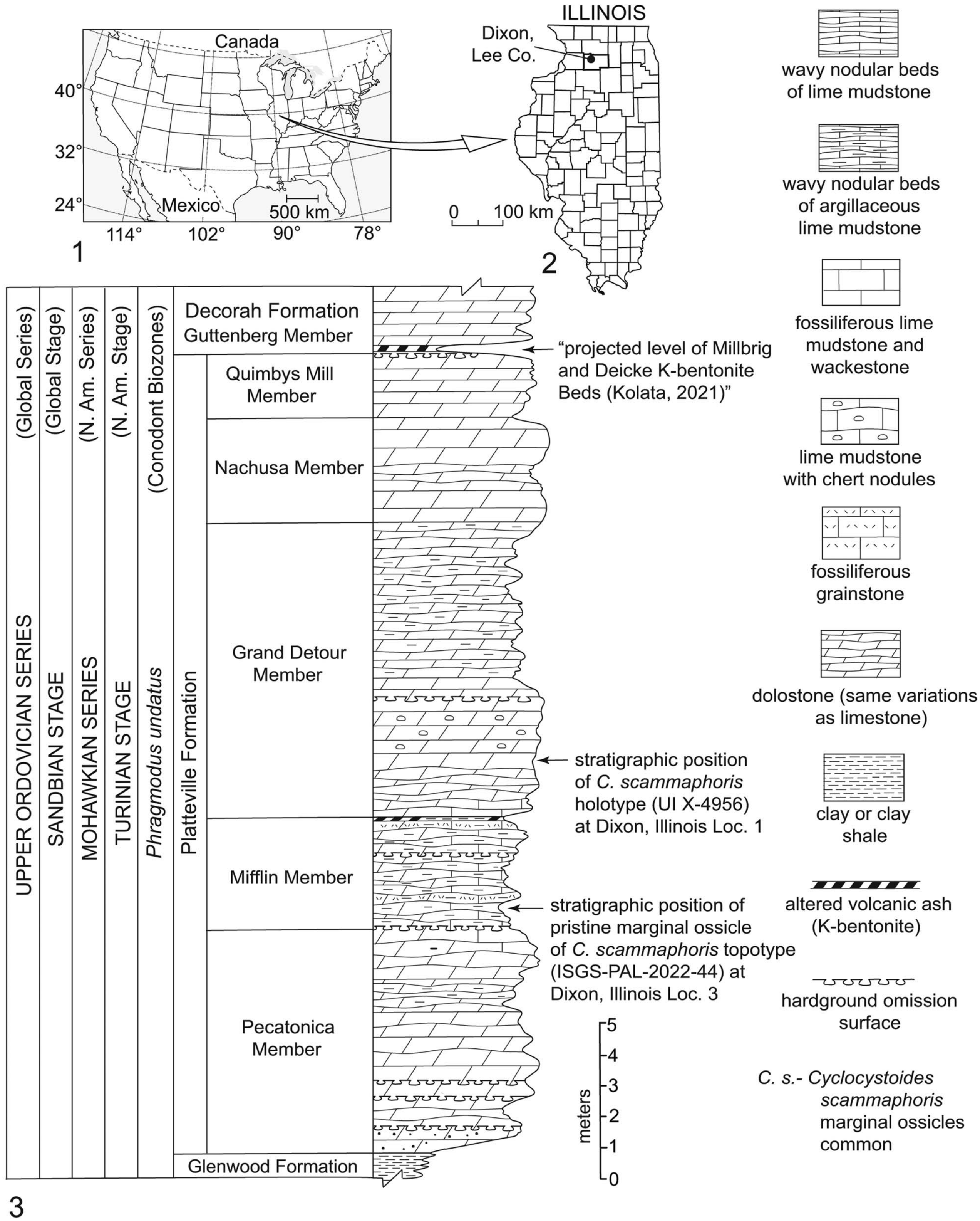

Figure S1. Maps and stratigraphy: (**1**) USA with position of Illinois; (**2**) state of Illinois with location of city of Dixon in Lee County; (**3**) stratigraphic column based on drill core of Illinois State Geological Survey No. 1 Jerry Stuff exploratory boring, locality 7. Lithologic symbols shown on right side.

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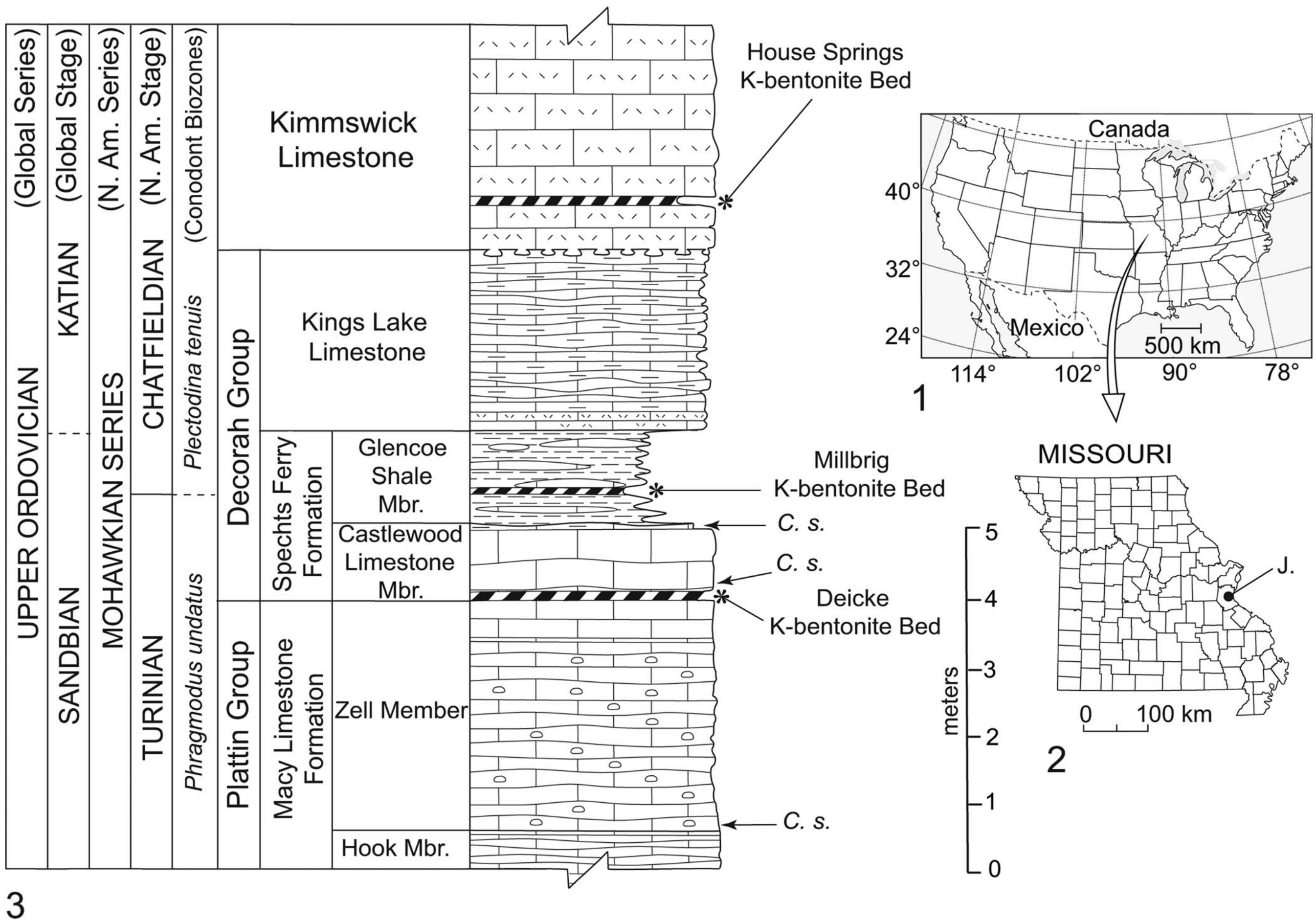

Figure S2. Maps and stratigraphy: (**1**) USA with position of Missouri; (**2**) state of Missouri with location of Jefferson County (J) where specimens of *Cyclocystoides scammaphoris* were collected; (**3**) stratigraphic column based on outcrop exposed on Fox Creek Road 1 km west of Allenton Road in Eureka, St. Louis County, Missouri, locality 7. The stratigraphic succession, thickness of beds, and cyclocystoid-bearing stratigraphic horizons are typical of those occurring in east-central Missouri. Lithologic symbols as in Figure S1.

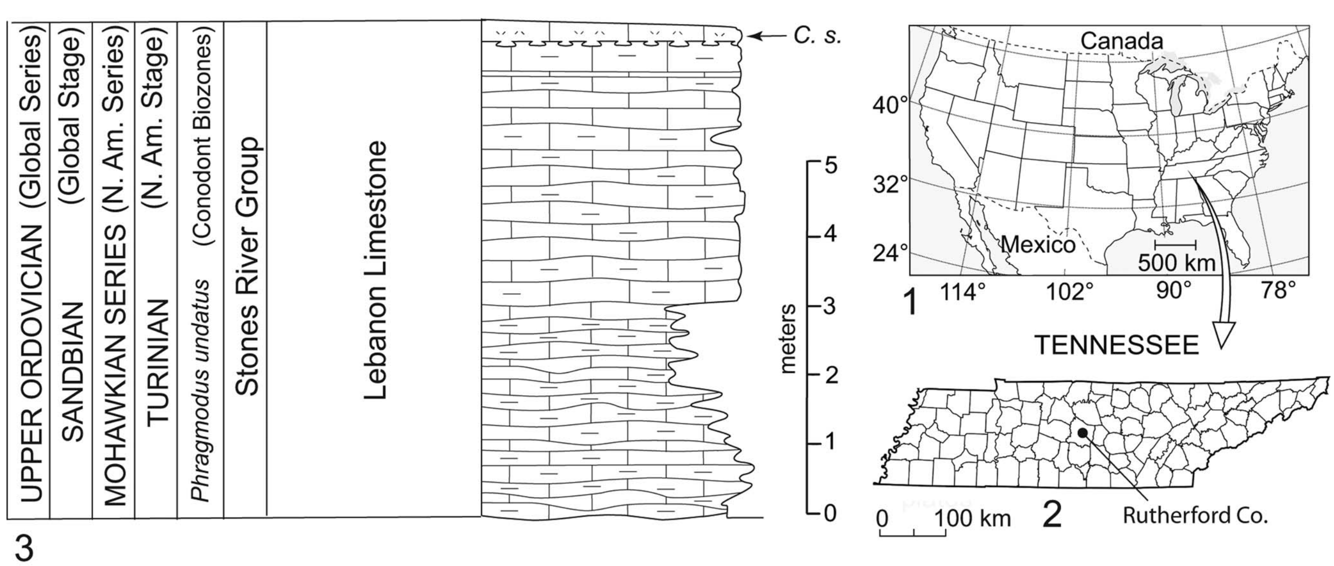

Figure S3. Maps and stratigraphy: (**1**) USA with position of Tennessee; (**2**) state of Tennessee with location of Rutherford County; (**3**) stratigraphic column based on outcrop exposed on east side of I-24, 2.8 km north of Hoovers Gap exit (approximately 15 km southeast of Murfreesboro), Rutherford County, Tennessee, locality 8. Stratigraphic succession, thickness of beds, and cyclocystoid-bearing stratigraphic horizon are shown. Lithologic symbols as in Figure S1.

Central Tennessee locality

8. Roadcut on I-24, 2.8 km north of Hoovers Gap exit (approximately 15 km southeast of Murfreesboro), Rutherford County, Tennessee; 35°41′38.40′′N, 86°17′51.93′′W. *C. scammaphoris* found in the lower member of the Lebanon Limestone of the Stones River Group.

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